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Changes in group size in *Kobus kob kob* (Bovidae) in the Comoé National Park, Ivory Coast (West Africa)

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Abstract

During a 30 month study in the Comoé National Park, Ivory Coast, it was revealed that median size of kob antelope groups which contained a majority of adult females varied between as well as within seasons. Group size was smallest at the height of the rainy season and greatest at the beginning of the rainy season. Whereas increase in group size in the beginning rainy season might have been related to the improving feeding conditions and to reproductive behaviour, reduction of number of animals per group at the height of the rainy season was probably influenced by grass height. In addition to grass height, other factors influencing visibility such as vegetation density, time of the day (day/night) and moon light intensity at night effected group size. While long term trends in group size changes are effected by food availability and reproduction, we assume visibility to be the proximate factor influencing short term (1–24 hours) group size changes in kobs in the study area. We presume avoidance of predator attacks to be the ultimate cause for these changes.

Key words: *Kobus kob*, Ivory Coast, group size variability, visibility

Introduction

During a study on the eco-ethology of kob antelope (*Kobus kob kob*) in the Comoé National Park. Fischer (1998) found that groups dominated by females in terms of number showed a high fluidity in group size Approximately 70% of all groups encountered contained a majority of adult females and were therefore called female groups. Only those groups have been included in our investigation. Composition of such groups could never be predicted. Beside observed short-term fluidity of the groups, long-term changes in the average group size were obvious in the course of the year. The aim of our study was to collect information about group size changes and come up with possible explanations for the underlying forces.

Materials and methods

Study site

The data were collected during 30 months of field observations of kob antelope in the Comoé National Park (Fischer 1995, 1996, 1998). The park is located in the north-east of the Ivory Coast between 9°6′ N–8° 5′ N and 3°1′ W–4°4′ W. The study area is situated in the southern part of the park, at the eastern bank of the Comoé river (Fig. 1).

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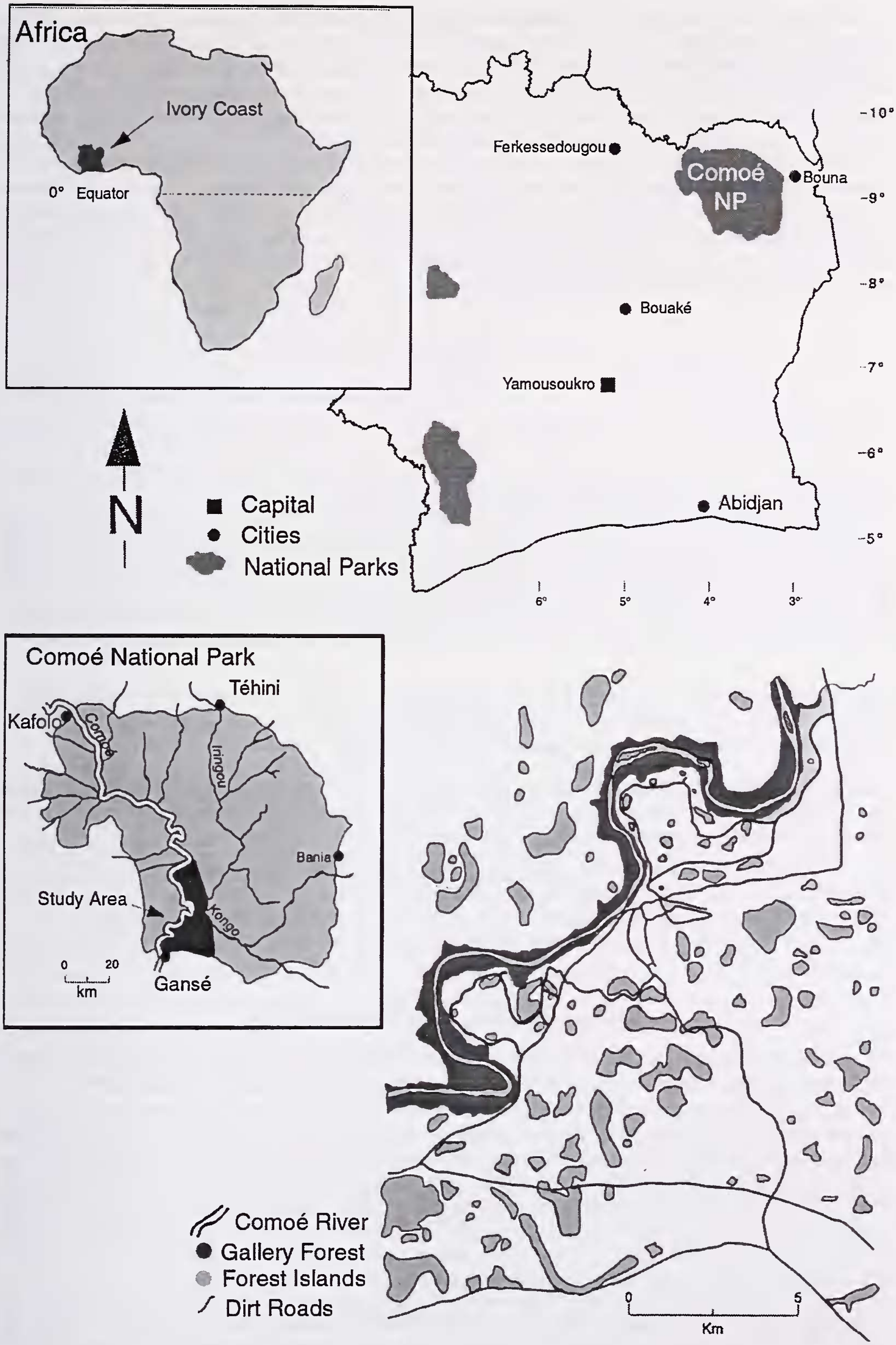

Fig. 1. Map of Africa and Ivory Coast. Below map of the Comoé National Park and the observation area.

The habitat is a tree-shrub savannah, which has been described in detail by Porembski (1991). Open areas are dominated by the following grasses *Loudetia simplex*, *Schizachyrium sanguineum*, and *Andropogon canaliculatus*. The Comoé river is bordered by gallery forest 50 to 200 m in width. Great variation in rainfall patterns within and between years, differences in vegetation height between the seasons and annual bush fires make the southern part of the Comoé National Park a strongly seasonal habitat with unpredictable and sometimes rapidly changing conditions.

Natural predators of the kob, as e. g. leopard (*Panthera pardus*), hyena (*Crocuta crocuta*), and lion (*Panthera leo*) occur in the study area, with the latter being very rare. No signs of caracal (*Felis caracal*), side-striped jackal (*Canis adustus*) or wild dog (*Lycaon pictus*) could be found, although the Comoé National Park is in the range of their distribution area (Haltenorth and Diller 1977; Kingdon 1997). The presence of serval (*Felis serval*) is doubtful. There is heavy poaching on kob antelopes with severe impact on the population (Fischer 1996).

Seasons

Most of the rains (89.7% ± 2.3%) in all years of the study period fell between April and November. The duration and intensity of the dry and rainy seasons in the study area show a high variability between years. Rain may fall in all months during the dry season, may be very rare during certain months of the rainy season, and is highly variable in temporal as well as spatial distribution and quantity. The rainy season is interrupted by a short dry period in July.

Since ecological conditions changed considerably within the wet season, we did not only discriminate between the rainy and the dry season, but further divided the wettest months in two periods, called the beginning rainy season and the height of the rainy season. In order to faciliate data comparison between periods, we distinguished between three seasons of equal length. Even though only little rain fell in November, it was considered a wet month, since water was found in almost every pond in the savanna and the soil was moist. Table 1 shows the definitions for the three seasons.

Table 1. Definition and description of seasons for the southern Comoé National Park applied during the kob study. I = dry season; II = beginning rainy season; III = height of the rainy season; Tse-Tse density refers to the abundance of blood suckling flies of the genus *Glossina*.

season	period (months)	rainfall	grass height	grass age	water is available	Tse-Tse density
I	Dec–Mar	low	low	young	river only	low
II	Apr–Jul	high	intermediate	intermediate	river and savannah	intermediate
III	Aug–Nov	high	high	old	river and savannah	high

Animal observations and data sampling

Animals were observed and counted from a four-wheel-drive car on a 6.3 km long and 200 m wide road strip. Kob densities were calculated using King's road strip method (Mühlenberg 1993).

Social groupings were defined following Underwood's (1982) definition of ungulate groups. All animals closer than 50 m to their nearest neighbour moving in the same direction or synchronizing their behaviour otherwise were assumed to belong to one group. In all tests group sizes include all animals of such aggregations. Only groups with a majority of adult females were used in this study. These groups were then counted in total, including all members. Animals were identified and counted using binoculars (10×40 Zeiss). Occurrence of mating behaviour, group size and composition, as well as location in the area (category of vegetation density) were noted on a prepared form. Horn shape and dimension in males and body size in females were used to determine the animals' age, with the following classes being distinguished: adult females, adult males, subadult males, juvenile females, juvenile males and calves. Groups were also scanned for known individuals (13 adult males, 9 adult females, 2 subadult males) which could be recognised either by natural (ear notches, horn shape, colour) or artificial markings (ear tags, radio collars). Ear tags and radio collars were attached to animals captured in 1994, 1995, and 1996. Night counts were carried out using two 100 Watt headlights held up by two assistants from either side of the car to spot the animals by light reflection of their eyes. Observation distances ranged from less than 20 m up to 200 m (mean: 60 m).

To estimate vegetation density, the number of trees with a height of at least one meter was measured at 30 sites using the Point-Centred-Quarter-Method (Müller-Dombois and Ellenberg 1974). This led to the distinction of three different categories of vegetation density (open: < 0.5 tree/100 m^2; semi-dense: 0.5–5 trees/100 m^2; dense: > 5 trees/100 m^2).

Day/night comparisons were made between successive day/night periods, so that for each day sampled, only data from the following night were used in the analysis. Data collection at night took place in periods comprising one clear new or full moon night and the two preceding and following nights.

At night and during the day prostrate kobs got up within one or two minutes after a car stopped in their vicinity to look at the intruder. Counts in dense vegetation were performed at the beginning rainy season only, when grass height is not sufficient to conceal a standing kob. We therefore assume that only a negligible number of kobs have been overlooked.

Rainfall was measured to the nearest mm after every rain event and grass height to the nearest cm once per month at one site in the savannah. Mean rainfall and mean grass height per month were calculated from data collected in each month between March 1993 and Dezember 1998.

Statistics

All statistical tests are two-tailed and were performed with SPSS for Windows or calculated by hand. Medians are given with their 95% confidence limits. Kolmogoroff-Smirnoff-Test was used to compare different group sizes (Sachs 1984). Wilcoxon-Matched-Pairs-Test was used in the comparison of night and day data, to test if individually known females changed their preference for group size within 12 hours. Spearman-rank-correlation was performed to test if median group size was correlated with grass height or rainfall. Chi^2 test was used to test if distribution of reproductive behaviour in certain months differed from an equal distribution.

Results

Rainfall and Vegetation

Grass growth is triggered by annual burning of most of the savannah and is accelerated at the onset of the rainy season. Figure 2 shows the mean monthly rainfall and the mean grass height for 1993–1998. Total rainfall was 1032 mm in 1993, 856 mm in 1994, 1071 mm in 1995, 1124 mm in 1996, 1022 in 1997, and 1248 in 1998. During the five years of the study the following patterns of rainfall, water, and food availability were found: In January the dry season in the study area was at its peak. Water was still available in the Comoé River, but no free water occurred in the savannah. Up to 100% of the grass plains had usually been burnt by then and food was scarce since grass started to grow only slowly after the burns. Only in 1994 and 1998 rain did fall in January with 2 mm and 74 mm respectively. In February young grass still grew slowly, but with the beginning of the rains in March grass growth accelerated. Grass grew rapidly from March till May on all burnt plots. After the rains of February and March small ponds in the savannah were formed, usually only for a couple of days or even hours. Heavier rains in April filled ponds and pools in the savannah, and small streams began to run. Dependence of kob on drinking opportunities at the Comoé River lasted usually until April. Rains through October promoted grass growth until November. In December rain fell only in 1995 (10 mm) and 1998 (18 mm), and poachers started to burn the plains where grass was already dry.

Population density

The population of kob antelope in the study area has declined by about 80% since 1978 and during the study period from 8.6 ± 0.53 to 6.1 ± 0.7 animals per km^2 (GTZ/FGU 1979; Fischer 1998). This decline is presumably due to intensive poaching in the area (Fischer 1996).

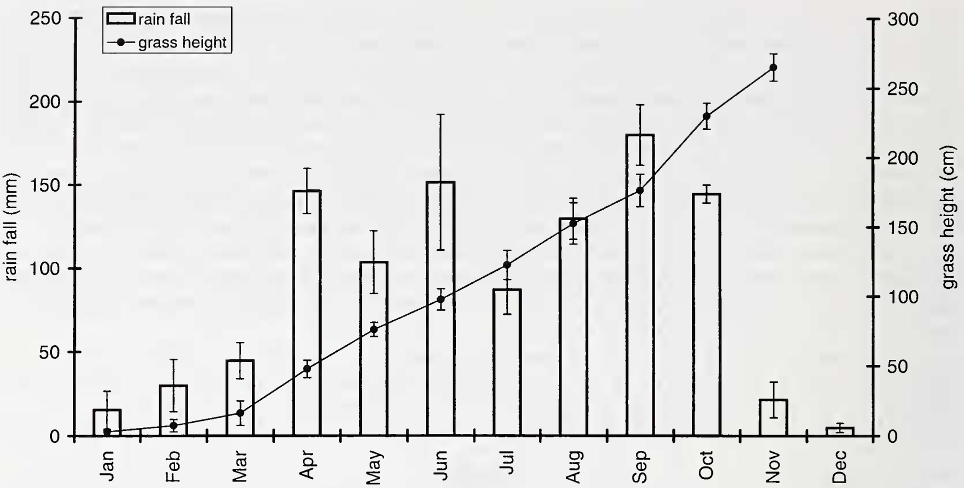

Fig. 2. Mean monthly rainfall and mean grass height in the study area in the southern Comoé National Park during the study period. Vertical bars indicate standard errors.

Reproductive behaviour

Mating and calving was observed throughout the year. Compared to the annual mean an increase of mating behaviour was observed in February (Chi^2 6.2487 > 3.8415, $p < 0.05$) and March (Chi^2 6.8514 > 3.8415, $p < 0.05$). Fewer matings took place in June (Chi^2 4,9307 > 3.8415, $p < 0.05$). In all other months mating behaviour showed no deviation from the annual mean.

Annual cycle of group size

Females were found alone or in mixed groups of up to 72 animals. Median size of such groups encountered during daytime changed in the course of the year, leading to a rather regular annual cycle which is shown in figure 3 in relation to grass height. Combining the data of all study years, the following pattern was revealed: female kob aggregated in groups with a median of four animals in January and February. The size of the average female group rose in March to a median of five and peaked in April and May resulting in groups of about six animals. After this peak the number of animals per group declined constantly to a median of five in June, four in July and August, three in September and two in October. Lowest numbers occurred in November with the median of one animal per group. We did not collect data for group size in December.

Median group size was largest at the beginning of the rainy season in April and May when grass on fresh burns grew rapidly to medium heights. The smallest groups were found at the end of the rainy season in November when grass was dry and of maximum height resulting in reduced visibility. It was neither correlated to grass height (Spearman-rank-correlation: $n = 30$, $p = 0.176$, $r^2 = -0.254$) nor to rainfall (Spearman-rank-correlation: $n = 30$, $p = 0.528$, $r^2 = 0.120$). Kolmogoroff-Smirnoff-Test showed that median group size differed significantly between the beginning (April–July) and the end (August–November) of the rainy season (Tab. 2). Since median group size was lowest when visibility was scarce due to grass height, we investigated whether reduced visibility in general leads to a reduction in group size. We collected data on size of female groups with relation to grass height, vegetation density, time of day, and light intensity during nights. Medians with their 95% confidence intervals are shown in figure 4 for all comparisons.

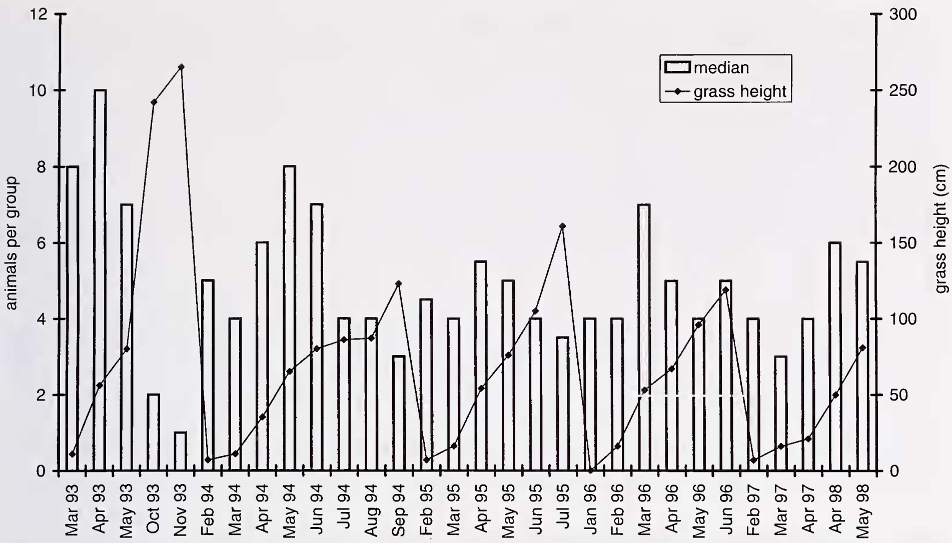

Fig. 3. Annual cycle of median group size of *Kobus kob kob* and grass height for the 30 months sampled in the southern Comoé National Park.

Table 2. Factors influencing group size of *Kobus kob kob* in the southern Comoé National Park including results of Kolmogoroff-Smirnoff-Tests

factors compared	D alpha	D^	significance	group size larger at
season II versus season III	0.088	0.324	+	season II
day versus night	0.122	0.297	+	day
full moon versus new moon nights	0.023	0.327	+	full moon
full moon versus new moon days	0.167	0.103	–	no difference
dense versus semi dense	0.135	0.042	–	no difference
dense versus open	0.123	0.133	+	open
semi dense versus open	0.095	0.139	+	open

Variation between successive day and night periods

It was tested whether size of female groups varied between successive day and night periods. Included in this analysis are all nights independently of the phase of the moon. In 68 cases in which known individuals were observed twice during 12 hours it could be shown that group size had changed within this time span in 88.2% of all cases, and was significantly smaller during nights (Wilcoxon Matched-Pairs Signed-Rank Test, $Z = -0.3267$, $p < 0.05$). In some cases it was also observed that known females encountered at daytime joined another group at night. This sometimes led to a group of equal size but different composition at night than during day. If these changes are taken into consideration as well, group size and/or group composition changed in more than 90% of all observed cases within 12 hours. Hence day and night counts of groups and group size were

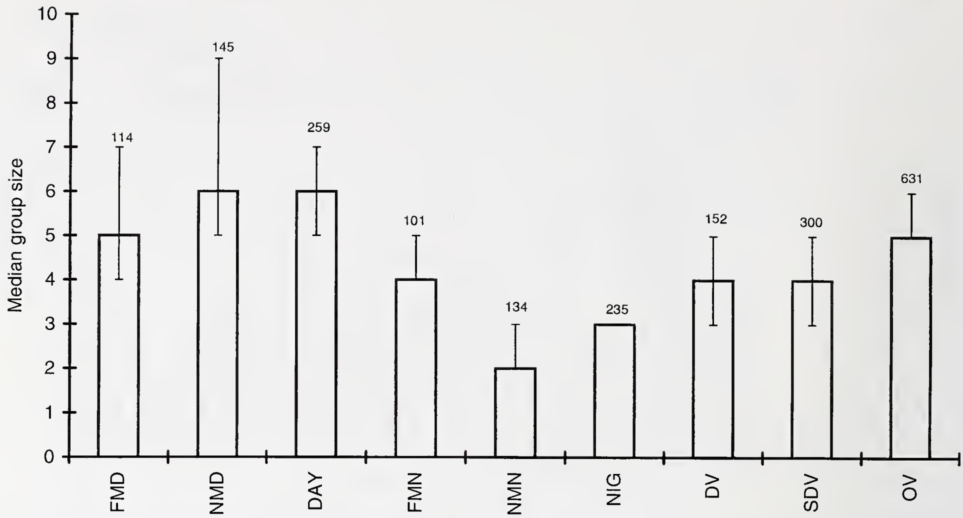

Fig. 4. Median group size of *Kobus kob kob* in the southern Comoé National Park according to various outer parameters related to visibility. Vertical bars indicate 95% confidence limits. Figures above bars give the number of groups included in the analysis. FMD = full moon day; NMD = new moon day; DAY = daytime (6:00 a. m. – 6:00 p. m.); FMN = full moon night; NMN = new moon night; NIG = nighttime (6:00 p. m. – 6:00 a. m.); DV = dense vegetation; SDV = semi dense vegetation; OV = open vegetation.

assumed to be independent of each other, although some members of groups might still have been the same individuals. Kolmogoroff-Smirnoff-Test revealed that groups that contained only unknown females were significantly larger during days compared to nights (n = 494).

Variation between new moon and full moon nights

To test if other factors might have caused group size changes between full moon and new moon periods, group size data collected during nights were compared between full and new moon phases.

Group size was significanfly larger during full moon nights compared to new moon nights. However, no significant differences could be found between full moon and new moon days (Tab. 2, and Fig. 4).

Vegetation density

Of the 1.080 groups observed, 58.1% were found in open vegetation, 27.8% in semi-dense, and 14.1% in dense vegetation.

Kolmogoroff-Smirnoff-Test revealed significant differences in group size between semi-dense and open vegetation as well as between dense and open vegetation. No significant difference between group sizes in dense and semi-dense vegetation could be found.

Discussion

Seasonal changes in African ungulate groups, as we observed, have been detected by Rodgers (1977) and Underwood (1982). Underwood (1982) was able to correlate increasing group sizes with rainfall and breeding cycles in different ungulate species. Rodgers (1977) emphasised the effects of social and reproductive behaviour on group size and held territorial behaviour in male impala (*Aepyceros melampus*) and herding activity in male wildebeest (*Connochaetes taurinus*) responsible for increases in group size during the rut. McNaughton (1984) showed that ungulates sometimes establish grazing lawns where grass remains short and biomass high for long periods, thus improving foraging conditions compared to surrounding savannah areas and leading to an increase in group size. Duncan and Vigne (1979) found that group size of horses increased in the presence of large amounts of blood-sucking flies. Do the above results explain our findings in kob antelope?

Group size changes in our study were not correlated to rainfall, and no clear rutting season of kobs exists here. Due to the low population density in our study area, ungulates were not able to establish grazing lawns. However, the beginning of grass growth in February which resulted in small patches of young grass on fresh burns led to aggregations of kob on such sites at the beginning rainy season, which might have added to an increase in group size during that time. Additionally larger groups in February and smaller ones in June might partially be explained by reproductive behaviour (observed more often in February and less in June).

Nevertheless, such behaviour cannot explain the changes of group size in other months. The abundance of tsetse flies (*Glossina* spec.) shows a high variance between seasons in our study area. The tsetse population collapses as soon as the grassland in the area is burnt in December and January, then begins to rise again with the first rains, leading to constantly increasing numbers of tsetse flies from March onwards. Highest numbers can be found between July and November, which following Duncan and Vigne (1979) should lead to an increase in ungulate group size during that time. Instead median group size in the studied kob population decreased from June onwards and was smallest in November.

Since kobs have to drink daily and water availability in the area changes between seasons, it would be conceivable that groups are largest when water is scarce and kobs gather at the rare drinking sites. Since all drinking sites during the dry season are located in the riverbed of the Comoé and can only be reached by traversing the gallery forest, the preferred habitat of leopard and hyena, larger groups during that time may also form in order to reduce vulnerability to those predators. Nevertheless, no correlation between rainfall and hence water availability and group size was found and median group size was smallest at the end of the year when water was only available in the Comoé river.

While increase in group size between February and March might partially be explained by feeding conditions and reproductive behaviour, our findings excluded food and water availability, reproductive behaviour and attacks of blood sucking flies as single explanations for decreasing group size later on. We therefore believe that the hypothesis best fitting our results is, that decreasing visibility due to the higher grass was the reason for smaller median group sizes from June to November.

Provided our assumption is correct, kobs should reduce group size not only in dependence of grass height, but also under other conditions where visibility is otherwise low. According to the hypothesis, groups would be expected to be significantly smaller in dense vegetation, at night and here especially in dark nights (new moon nights). These expectations proved to be correct. However, no difference in size could be found when groups in dense and semi-dense vegetation were compared. Apparently kobs do not distinguish between these two vegetation density categories.

Similar influences of vegetation density on group size was shown by Leuthold (1970) for impala, by Deutsch and Weeks (1992) for Uganda kob, and by Evans (1979) for kudu (*Tragelaphus strepsiceros*). Clarke et al. (1995) demonstrated that eastern grey kangaroos (*Macropus giganteus*) reduced their group size during nights.

Aggregation is generally considered to serve as a protective mechanism against predators hunting by sight (Hamilton 1971; Bertram 1978). If groups are to be attacked, the single individual might decrease the probability to fall victim to the predator due to effects of dilution, position and confusion (Vine 1971; Pulliam 1973; Treisman 1975; Dehn 1990). Under certain circumstances, such as wide and open areas, larger groups might detect an approaching predator earlier or might even be avoided by the predator as Fitz-Gibbon (1990) showed for Thomson's (*Gazella thomsoni*) and Grant's gazelles (*Gazella granti*) hunted by cheetah (*Acinonyx jubatus*). Whereas advantages of dilution and confusion effects increase with larger group size, probability of early predator detection increases with better visibility. Deutsch and Weeks (1992) showed for example that lion hunting success on kob increased with grass height and thicket density. Certain disadvantages are correlated with staying in larger groups when visibility is low. Such groups provide stronger auditory and olfactory signals, are more conspicuous and can therefore be more easily detected by predators like leopards which use those signals to find their prey (Treisman 1975). Additionally, in cases of low visibility prey might depend on acoustic perception of the predator which might be more difficult when groups are larger and thus noisier. There should be a trade-off between advantages and disadvantages of grouping depending on visibility factors. Group size should increase: in open vegetation, in lower grass, during daytime and during full moon nights. Since all statistical tests led to significant results clearly corroborating these predictions, it is assumed that visibility is a factor strongly influencing group size. The preference of kob antelope for high visibility locations was also shown by Deutsch and Weeks (1992), who proved that kob antelopes preferred high visibility leks and territories. The variation of group size in response to visibility factors is thus evaluated as an evolutionary adaptation to the presence of predators. Although lions are rare and wilddogs are extinct in the Comoé, there remain leopard, hyena and human hunters in high abundance. The most effective and dangerous predator of kob antelopes in the study area is man, who hunts during days and more recently during nights as well. Initial results of Gross (pers comm.), tracking five radio collared leopards in the study area showed that these animals have a reversed short-term habitat preference compared to kob antelopes All leopards used open areas of their home-range at new moon nights which they avoided during full moon nights. Leopards also changed their activity pattern in response to season. They were nocturnal at the beginning of the year and switched to be active during days as soon as grass grew higher from June/July onwards.

Because of the low kob population density in the study area, some of the disadvantages of living in groups like increased competition for food resources do not fall into account. This holds especially true because population density dropped about 30% within the last three years without showing any influence on the kobs' grouping behaviour (Fischer 1996).

We conclude that group size is strongly influenced by visibility factors resulting in larger groups when visibility is good. Seasonal changes of group size in kob antelope might well be additionally influenced by other factors related to food availability or reproduction. Fresh grass supply is probably the most important reason for increasing group size at the beginning rainy season. The open herd structure of kob antelopes facilitates seasonal as well as short term changes in group size (Rodgers 1977; Evans 1979). As the cause for these predictable changes in group size, predator avoidance is discussed. The advantages of staying in a large group of conspecifics might be reversed in cases of low visibility due to the hunting pattern of predators who depend at least partially on acoustic perception under these conditions. In the kobs studied here, anti-predator behaviour against hyena, leopard or lion attacks as well as human hunting pressure might have been the reason for grouping and group size changes. Due to heavy poaching on kob antelopes in the Comoé National Park, man is the most dangerous and effective predator of kobs, and has already influenced their behaviour (Fischer and Linsenmair 1999).

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Zusammenfassung

Veränderungen der Gruppengröße von Kobus kob kob (Bovidae) im Comoé Nationalpark, Elfenbeinküste (Westafrika)

Im Rahmen einer 30 monatigen Studie im Comoé Nationalpark, Elfenbeinküste, wurde der Einfluß verschiedener äußerer Faktoren auf die Größe von Gruppen weiblicher Kobantilopen untersucht. Die Größe solcher Gruppen schwankte sowohl zwischen als auch innnerhalb von Jahreszeiten. Sie war am kleinsten zur Hochregenzeit und am größten zu Beginn der Regenzeit. Während Kobantilopen am Anfang der Regenzeit, im Zuge der Fortpflanzung und bei einem verbesserten Nahrungsangebot, größere Gruppen bildeten, stand die Abnahme in der Hochregenzeit vermutlich mit den schlechteren Sichtverhältnissen, hervorgerufen durch hohes Gras, in Zusammenhang. Innerhalb kürzerer Zeiträume hatten Faktoren wie Vegetationsdichte, Tageszeit (Tag/Nacht) und die Mondphase (Vollmond/Neumond) einen Effekt auf die Gruppengröße, wobei schlechtere Sichtverhältnisse zu einer Verringerung der Gruppengröße führten. Wir vermuten, daß bei den Veränderungen der Gruppengröße zwischen Jahreszeiten zusätzlich zu den Sichtverhältnissen die Nahrungsverfügbarkeit und das Fortpflanzungsverhalten eine Rolle spielen, während kurzfristige Schwankungen der Gruppengröße von Kobantilopen (innerhalb von 1–24 Stunden) ausschließlich von den Sichtverhältnissen beeinflußt werden. Den Grund für denWechsel der Gruppengröße in Abhängigkeit von den Sichtverhältnissen sehen wir im Zusammenhang mit derVermeidung von Angriffen großer Beutegreifer.

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